THE ROLE OF SCOUTING IN SLAVE RAIDS BY *POLYERGUS BREVICEPS* (HYMENOPTERA: FORMICIDAE)*

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Introduction

The formicine ant genus *Polyergus* contains four species, all of which are obligatory social parasites of the related genus *Formica.* Slave ants are obtained during group raids, in which a swarm of *Polyergus* workers penetrates a nest of *Formica,* disperses the adult workers and queen, and carries off the pupal brood (Topoff et al. 1984, 1985). Although many of these pupae are subsequently consumed in the slave-maker's nest (Kwait and Topoff 1984), a significant portion of the *Formica* brood is reared through pupal development. Workers eclosing from this pupal population subsequently perform their typical functions (i.e., foraging, feeding, nest defense) as permanent members of a mixed-species nest.

Ever since the pioneering studies on *Polyergus rufescens* by Huber (1810) and Emery (1908), on *P. lucidus* by Talbot (1967) and Harman (1968), and on *P. breviceps* by Wheeler (1916), it has been well known that slave-making raids are usually initiated by a small group of workers called scouts. These individuals locate target colonies of *Formica,* return to their colony of origin, recruit nestmates, and lead the raiders back to the *Formica* nest. Despite the generalization that *Polyergus* slave raids are typically preceded by scouting, virtually no field studies exist showing the actual paths travelled by scouts, or their overall importance in initiating slave raids. In their study of laboratory colonies of *P. lucidus,* Kwait and Topoff (1984) found that most raids were indeed directed towards

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Formica schaufussi nests that were scouted on the same day. And in a preliminary field study, the removal of scouts on each of 3 days in the field resulted in the absence of slave raids.

In this paper we report the results of longitudinal field studies on two colonies of the western slave-making ant *Polyergus breviceps.* In the first study, we discovered that scouts use a biphasic search strategy, consisting of an initial linear component, followed by random search within a limited sector. An additional finding was that scouts may use three different routes on the outbound run, return trip, and slave raid respectively. In the second study, in which we removed all scouts during a period of 19 days, we verified their importance for raid onset.

Path of Scout

Materials and methods

All studies on scouts were conducted at the Southwestern Research Station, located 5 km west of Portal, Arizona. At an altitude of 1646 m, the ground in this habitat is covered with bunch grass and contains extensive leaf litter from alligator juniper, Arizona oak, and Chihuahua pine. The period for this study was July 10–30, 1986. To facilitate the detection of *Polyergus breviceps* scouts, one colony was enclosed by a circular, aluminum-flashing fence (15 cm high), using the *Polyergus* nest entrance as the center. The radius of the enclosure was 7 m, which insured that all ants reaching the fence were scouts (and not the circlers, which routinely emerge and mill around the nest entrance prior to raiding). To enable scouts to move in and out of the enclosure, the fence contained four gaps (15 cm wide) at 90-degree intervals, starting at the north end. Beginning at 1400 hr (MST), one person walked continuously around the circular fence. Scouts reaching the fence usually ran along the inside wall, and left the enclosure immediately upon encountering the nearest gap. Sometimes, a scout ran back and forth along the same small section of the fence's inner wall. On these occasions, a garden trowel was placed in the scout's path. When the scout moved onto the trowel, it was lifted and placed on the ground on the outer side of the fence. The path of each scout was marked by placing the stick end of cotton swabs (painted yellow and numbered sequentially) into the ground behind the scout, at approximately 1-m intervals. Because of the grass and leaf litter, this

procedure required two persons, the first to constantly monitor the scout's path, and the second to place the numbered markers. Using a compass and a rolling measuring wheel, a map was made depicting the scout's path.

Results

During the three-week period of this study, 18 scouts were followed on 12 different days. Of these 18 scouts, five were tracked only on their outbound trip to a target colony of *Formica gnava.* For three other scouts, we succeeded in following their return trip as well. On five occasions, our tracking was abruptly halted when the scout was seized and killed by a spider. The remaining five scouts disappeared beneath the leaf litter before reaching a target colony.

The outbound paths of all scouts consisted of two distinct phases. Because of the essential similarity in movement among the scouts, the route illustrated in Figure 1 can serve as a typical example of scouting behavior. The target *Formica* nest on this day was located approximately 40 m to the west of the *Polyergus* nest. Phase one of scouting began when individuals left the swarm of ants circling around the nest, and moved in a relatively constant compass direction. For the scout on the afternoon of July 23, this straight run extended about 30 m to the west (the range for phase-one scouting on all days was 25–45 m). During this phase the scouts ran continuously, without stopping to search for *Formica* colonies. The second phase of scouting involved a qualitatively different pattern of movement, with scouts changing direction after running small distances over all compass directions. More importantly, it was only during this second phase that scouts periodically stopped and searched beneath rocks and patches of leaf litter. On July 23, this searching phase extended the scout's path for an additional 10 m to the west, with the north and south displacement combined covering about 14 m. Thus the searching phase of this particular scout covered an area of approximately 140 m^2.

A representative map of the complete sequence of successful scouting, followed by a slave raid, is illustrated in Figure 2. To clarify the distinctness of the paths, the erratic phase-two movements of the scout were replaced by a line extending from the end of the phase-one run, directly to the target nest. The most significant finding here is occurrence of three non-overlapping routes for the outbound run, return trip, and slave raid respectively. After locating

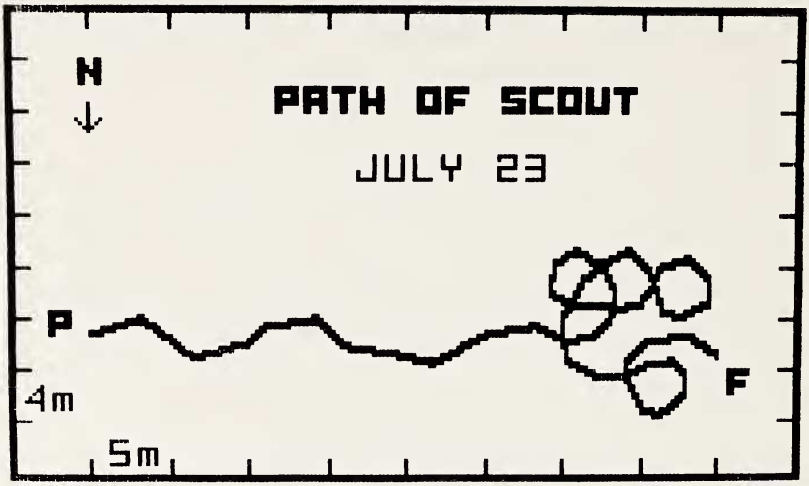

Fig. 1. Outbound path of *Polyergus* scout, consisting of a linear phase, followed by a circuitous (searching) phase. Scales of distance are shown at the lower left corner. N = north; P = location of *Polyergus* nest; F = location of *Formica* nest.

a *Formica* nest, the scout's return route paralleled its outbound course, but was displaced about 1 m to the east. The slave raid back to the *Formica* colony was displaced an additional 2 m to the east. Because the scout was not marked, we can not be certain that the slave raid was led by the same individual. Nevertheless, our previous studies with marked scouts (Topoff et al. 1984) indicate that successful scouts of *P. breviceps* typically run (at least intermittently) at the head of raid swarms.

Importance of Scouts for Slave Raids

Materials and methods

To determine the importance of scouts for initiating slave raids, another aluminum-flashing fence (15 cm high, 7 m radius, and containing four exits spaced at 90-degree intervals) was constructed around a second colony of *P. breviceps*. Every afternoon, from 1400 hr to 1800 hr, the perimeter of the enclosure was continuously monitored for the presence of scouts. For each scout, we recorded the time of arrival at the fence and the compass direction in which it was travelling. Each scout was then removed and placed in a holding container until the end of the day, at which time all the captured

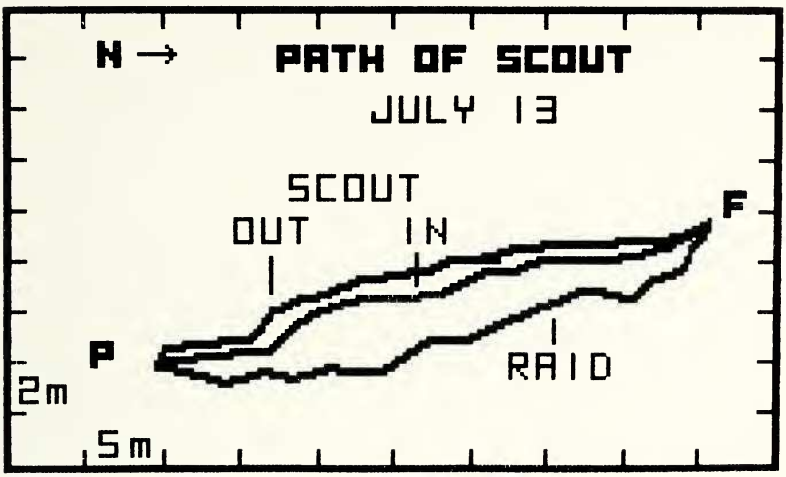

Fig. 2. Comparison of routes taken by *Polyergus* scout during outbound trip, return run, and subsequent slave-raid. Scales of distance are shown at the lower left corner. N = north; P = location of *Polyergus* nest; F = location of *Formica* nest.

scouts were placed at the nest entrance. This procedure for eliminating scouting was repeated for 19 consecutive days during the period July 2–July 20. Starting on July 21, and continuing until August 4, the fence was removed to permit unlimited scouting. Without the barrier, it was not possible to determine accurately the number of scouts departing each day. During this phase of the study, we simply verified that scouting occurred, and noted the time of raid onset.

Results

A comparison of the frequency of slave raids by *P. breviceps* with and without scouts is summarized in Table 1. The Table does not include data from days when scouting was prevented by rain or heavy overcast. Slave raids occurred on only 2 of 11 days (18%) during the period of scout removal. The two raids that occurred on 7/12 and 7/20 were stopped at the fence (by sealing the exits) to ensure that no *Formica* pupae would be brought back to the nest. When the fence was removed to permit scouting, the frequency of slave raids jumped to 69%, as 9 raids were conducted on 13 different days ($\chi^2 = 7.4$, df = 1, $P < 0.01$). All but one of these raids resulted in the capture of *Formica* brood, and the only unsuccessful one (July 23) was aborted by an abrupt thunderstorm.

Table 1. Comparison of slave-raid frequency with and without removal of scouts

Date	No. of Scouts	Scouts Removed	Slave Raid
7/02	8	+	-
7/05	7	+	-
7/06	3	+	-
7/09	1	+	-
7/10	5	+	-
7/11	1	+	-
7/12	15	+	+
7/13	24	+	-
7/15	21	+	-
7/17	13	+	-
7/20	16	+	+
7/21		-	+
7/22		-	+
7/23		-	+
7/24		-	+
7/25		-	++
7/27		-	-
7/28		-	+
7/29		-	-
7/30		-	+
7/31		-	-
8/01		-	+
8/04		-	+

++ denotes two raids on same day

Discussion

Polyergus breviceps is similar to other obligatory parasites in that workers do not search for food. Nevertheless, the location of target nests by scouts can be thought of as indirect foraging, because much of the raided *Formica* brood is fed to the *Polyergus* workers and queen by their resident slaves. It is therefore not surprising that the searching pattern of *Polyergus* scouts illustrated in Figure 1 is almost identical to that described for the ant *Cataglyphis bicolor,* which forages alone for dead arthropods (Harkness and Maroudas 1985). In this desert-dwelling species, foragers also move away from the nest in a linear path, followed by random searching throughout a particular sector. *Cataglyphis* can measure angular directions from the pattern of polarized light (Wehner and Menzel 1969), so it could forage in a straight line until it found food, and then return to

its home nest on the same bearing. But Harkness and Maroudas (1985) show that the sideways search pattern decreases the time for the return trip, and the same argument could easily hold for *Polyergus.* In addition, the linear phase of the scout's route ensures minimum overlap among the sectors searched by all of the scouts on any given day.

Polyergus is also similar to *Cataglyphis* (and other formicine ants) in its ability to orient to polarized light, and we recently demonstrated that scouts use visual (and not chemical) orientation during their outbound and return run, and when leading the raid swarm back to the target nest (Topoff et al. 1984). Further support for this hypothesis stems from our map of the complete route taken by a scout on July 13 (Fig. 2), in which a different path was taken for each of the scout's three runs. A model based upon chemical cues would predict a single path for the outbound run, return trip, and slave raid respectively. However, because a chemical trail is deposited during the slave raid, we have not ruled out the possibility that scouts might follow trails deposited on previous days.

The initiation of slave-making raids by scouts has so far been reported for the myrmicine genera *Strongylognathus, Harpagoxenus, Leptothorax, Epimyrma,* and *Chalepoxenus,* and in the formicine genera *Formica, Polyergus,* and *Rossomyrmex* (see review by Buschinger et al. 1980). In both subfamilies, details of scouting show several striking similarities. For example, scouts of the myrmicine ant *Harpagoxenus sublaevis* tend to be experienced workers which are at least one year old (Buschinger 1968; Buschinger and Winter 1977). This is almost identical to the findings of Kwait and Topoff (1984) for the formicine *Polyergus lucidus,* in which ants functioned as scouts only during their second season after eclosing.

A second convergence between the two subfamilies concerns the role of scouting as a prerequisite for raiding. In a laboratory study of the myrmicine species *Harpagoxenus americanus* and *Leptothorax duloticus,* Alloway (1979) recorded a total of 23 slave raids. For both genera, scouting preceded all of the slave raids, and scouting never took place when raids did not occur. In a similar study with *P. lucidus,* Kwait and Topoff (1984) removed scouts from laboratory nests on each of 7 days, during which time no slave raids occurred. Furthermore, observations showed that 25 out of 27 raids were directed towards *Formica schaufussi* nests that were scouted on the same day. The remaining two raids were directed at target

nests that were scouted on the previous raid day. Our present field study with *P. breviceps* confirms the importance of scouting in the natural habitat. Because all scouts collected were returned to their nest in late afternoon, the colony's "interpretation" might have been that these scouts were simply unsuccessful in locating a colony of *Formica.* If this were the case, an adaptive colony response would be to send out more scouts on successive days. Note (in Table 1) that the number of scouts from July 7–July 11 ranged between 1 and 8, but that 15–25 scouts were collected between July 12 and July 20. It is plausible to hypothesize that the magnitude of scouting can be varied according to the colony's requirements, but a more rigorous, statistical analysis must await a larger sample size.

The data from July 12 and 20 also show that raids can be organized even when scouting has not taken place for at least one week, but we do not know how recruitment takes place when this occurs. When groups of *Polyergus* are led by same-day scouts, the raid typically mimics the biphasic nature of scouting. Thus, the raid starts with a relatively linear movement away from the nest, during which the swarm advances without stopping. This is followed by the second phase in which the ants periodically stop advancing, fan out in all directions, and search under rocks and leaf litter (Topoff et al. 1984). It will be interesting in future field studies to observe how slave raids proceed when not organized by same-day scouts. Under such circumstances, the linear phase of raiding might be eliminated, so that the *Polyergus* swarm is forced to advance in a more deliberate manner, with more numerous searching stops even close to the nest. Finally, formicine ants such as *Formica rufa* exhibit site allegiance, a process that is based upon individual memory of spatially-organized visual cues (Rosengren and Fortelius 1986). Using individually-marked *Polyergus,* we now plan to determine whether each scout has a particular compass direction and sector in which it regularly searches for *Formica* colonies.

Summary

Slave raids by *Polyergus breviceps* are initiated by one or more scouts which locate target colonies of *Formica gnava,* and recruit nestmates to participate in group raids. Field studies in southeastern Arizona showed that scouting comprises two distinct phases. The first is a linear movement away from the nest, during which no

searching occurs. This is followed by sideways movements, a phase characterized by intensive searching under rocks and leaf litter throughout a limited sector. Sometimes, the scout takes a different route on the outbound run, return trip, and slave raid respectively. The distinctness among these three paths is consistent with the hypothesis that scouts rely primarily on visual orientation. The importance of scouts was determined by their systematic removal, resulting in the absence of raiding on 9 out of 11 days. When scouting was subsequently permitted, raids occurred on 9 out of 12 days.

Acknowledgments

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